Simulating ungulate herbivory across forest landscapes: a browsing extension for LANDIS-II

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Introduction

Browsing ungulates (e.g., moose and white-tailed deer) can be important drivers of the structure and function of forest ecosystems. They modify plant growth and survival, successional trajectories, soil dynamic properties like carbon, nutrient cycles, and fire regimes (Fig. 1).

Fig. 1. Example deer browse damage.

Ungulates require large amounts of plant tissue to meet their daily energy requirements. For example, estimates of dry matter intake can be near 5 kg dry mass per day for white tailed deer and as high as 10 kg dry mass per day for moose.

We describe a new ungulate browse extension for the forest landscape simulation model, LANDIS-II (Scheller et al., 2007). The extension uses the biomass associated with annual net primary productivity (cohort biomass) as a common currency linking tree species cohort growth, ungulate populations, and browsing impacts.

The addition of the browse extension to the LANDIS-II framework enables investigation of interactions among herbivory, forest vegetation dynamics, soil carbon change and sequestration, other disturbances (e.g., wind, fire, insects, and harvesting), and processes such as climate change.

Poster Goals:

Demonstrate the extension within the framework of LANDIS-II and demonstrates adaptability of the extension to address effects of browsing via two case study applications.

- The first examines effects of browsing by white-tailed deer on aboveground biomass and forest succession in a northern hardwood forest (Allegheny National Forest (ANF), USA, Fig. 1) with persistently high rates of browsing.
- The second case study examines interactions between a moose population and spatial patterns of net primary productivity and available forage biomass and associated impacts on forest succession in a boreal landscape (Isle Royale National Park (ISRO), Michigan, USA, Fig. 2).

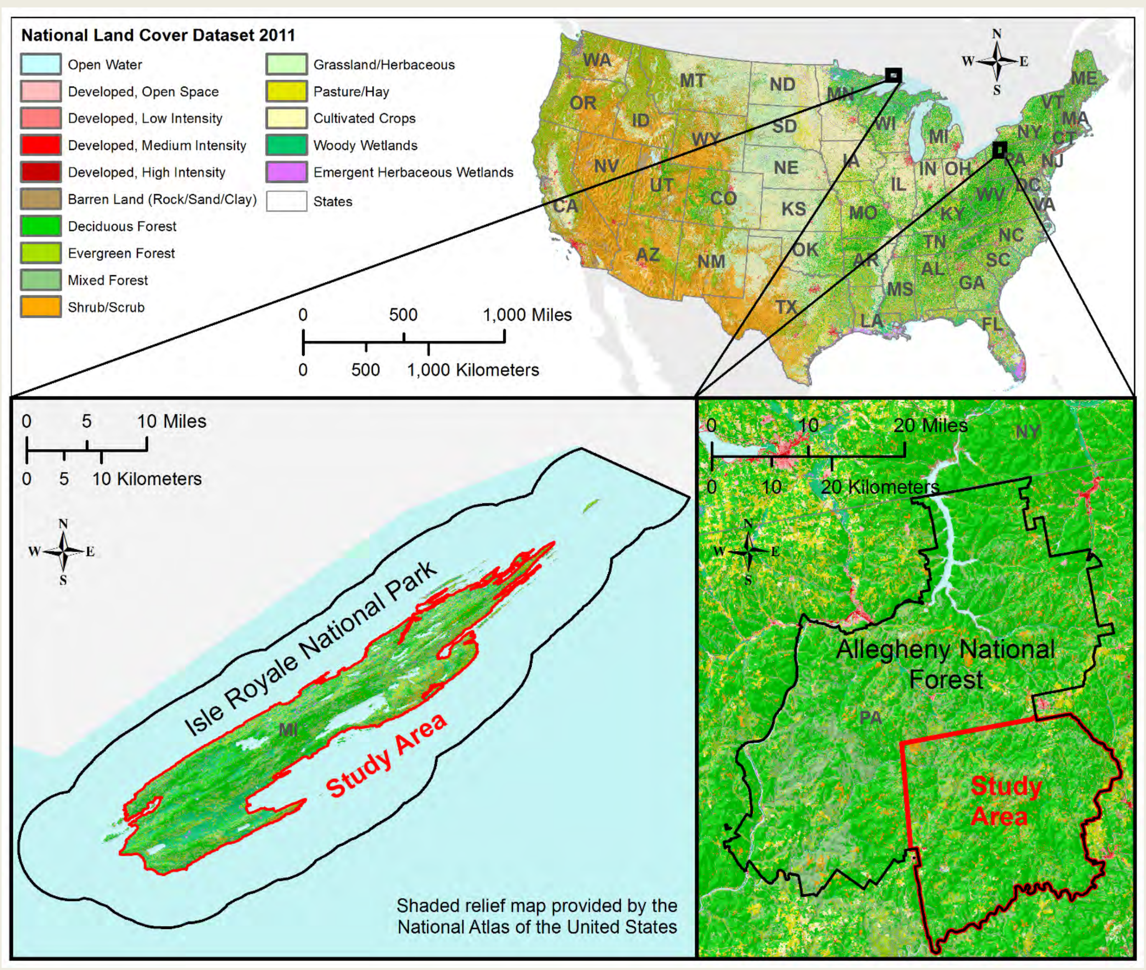


Fig. 2. The LANDIS-II Browse Extension landscape case studies: Allegheny National Forest in Pennsylvania, USA, and at Isle Royale National Park, Michigan, USA.

How the Extension Operates

Browsing by free ranging ungulates is often conceptualized as a series of decisions and processes nested in a hierarchy. In this extension, ungulate browse pressure is defined for population regions (zones) within the landscape, either externally as a browser density index (BDI) (ANF case study) or internally as a dynamic browser population (DBP) (ISRO case study).

Tree species dynamics at the site (cell) scale, combined with functions defining browse accessibility and selective preference define the amount and quality of browse on a given site. Intermediate to these two scales, neighborhood functions, typically at the scale of an ungulate home range, define how population density and browsing intensity (i.e., biomass consumed/removed) are distributed across a given population zone.

Once browsing intensity is distributed, forage biomass is removed from sites in proportion to the browse pressure, defined either externally (BDI) or internally (DBP), and according to user-defined species preferences and target removal rates derived from the literature.

Finally, herbivory influences the growth and development of browsed cohorts via the direct removal of biomass and additionally through user-defined species-specific growth response parameters. The sequence of model operations is shown in Fig. 3 and a complete list of user-defined model parameter estimates is provided in Table 1.

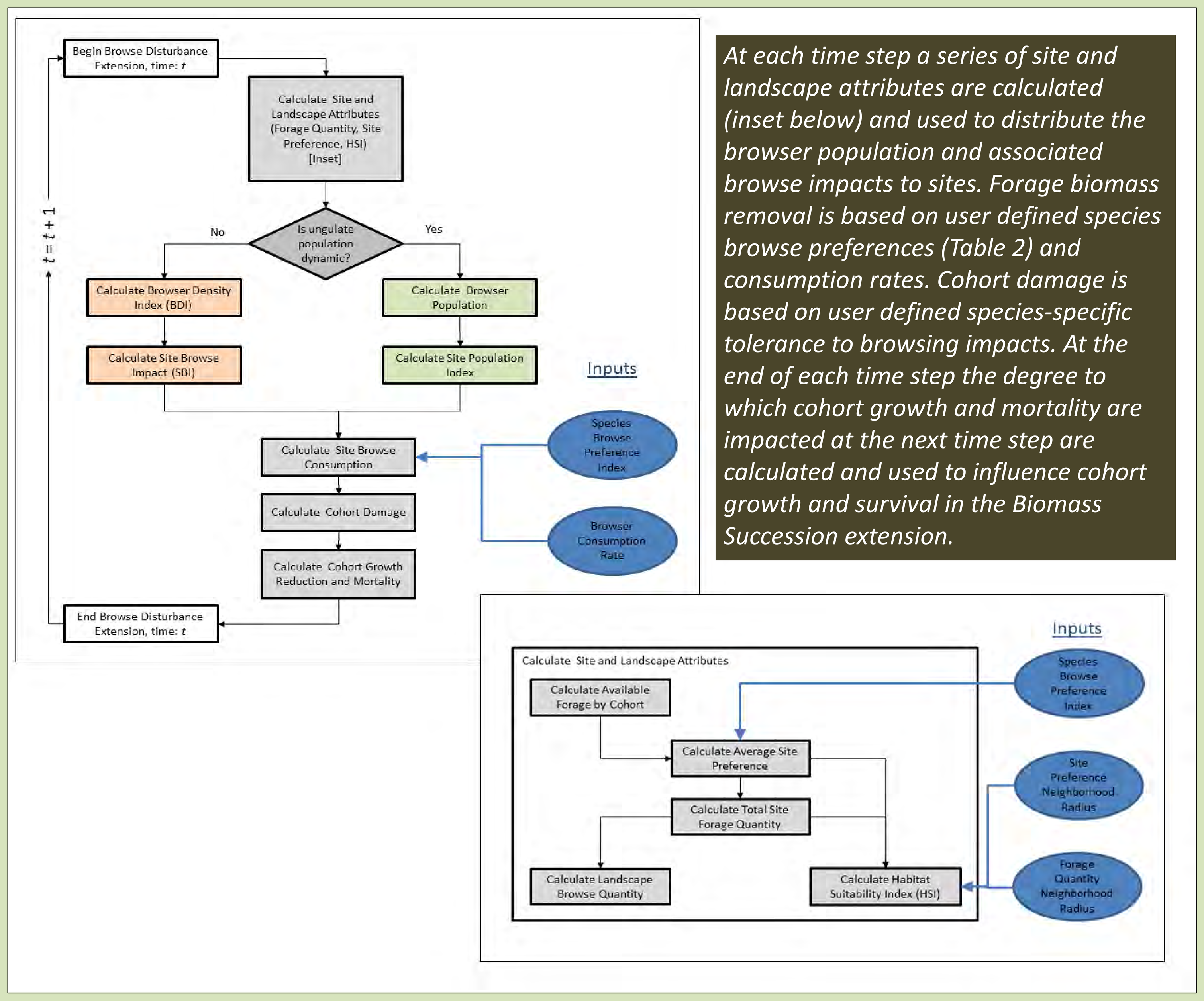


Fig. 3. The sequence of model calculations for the Browse Extension.

Component	Variable Name (Abbreviation)	Units	ANF	ISRO	Description
Available Forage Biomass	ANPPForageProp$_r$	Proportion	0.66	0.66	Proportion of ANPP that is available forage biomass
	MinBrowsePropinReach	Proportion	0.5	0.3	Minimum proportion of forage within reach for a cohort to be considered accessible
	BrowseBiomassThreshold	Proportion	0.05	0.05	Proportion of ecoregion maximum biomass when a cohort begins to escape browsing
	EscapeBrowsePropLong	Proportion	0.57	0.57	The proportion of the longevity of a species, at which cohorts escape browsing
	UseInitBiomassAsForage	Y/N	T	F	Use the total biomass of first-year cohorts as available, F-use only a fraction of ANPP from year 1 to 2 as available
Browse Biomass Removal	SpeciesPreference	Proportion	see table 2a	see table 2b	Target proportion of available forage biomass to be removed from a species, also used to rank species by preference
	ConsumptionRate	kg/animal/yr	N/A	2327	Annual consumption rate per animal
	Browser Density Index (BDI)	Proportion	0.45	N/A	Proportion of total available forage to remove
Effects of Browsing	Growth Reduction Threshold (GRT)	Proportion	see table 2a	see table 2b	Proportion of available forage biomass removed that triggers a reduction in ANPP at t+1
	Growth Reduction Maximum (GRM)	Proportion	see table 2a	see table 2b	Maximum reduction in ANPP at t+1 at 100% removal of available forage biomass
	Mortality Threshold (MT)	Proportion	see table 2a	see table 2b	Proportion of available forage biomass removed that triggers an increase in probability of mortality at t+1
	Mortality Maximum (MM)	Proportion	see table 2a	see table 2b	Maximum increase in the probability of mortality at t+1 at 100% removal of available forage biomass
Population Density	Initial Population Size (N_{init})	# animals	N/A	450 (~1 per km^2)	Initial population size, by population zone
	Population Growth Rate (R)	Rate	N/A	0.15-0.25	Min and Max population growth rate, by population zone
	Miscellaneous mortality (M)	Rate	N/A	0.0-0.1	Min and Max mortality rate, by population zone
	Predation (P)	Rate	N/A	0.03-0.1	Min and Max predation rate, by population zone
	Harvest (H)	Rate	N/A	0.0-0.0	Min and Max harvest rate, by population zone
Habitat Suitability/Population Distribution	ForageQuantity	Y/N, m	Y, 321	N	Utilize available forage biomass in calculating HSI, optional moving window size
	SitePreference	Y/N, m	Y, 1284	Y, 500	Utilize site preference in calculating HSI, optional moving window size
	CountNonForageSitePref	Y/N	N	N	include non-forage species in calculations of site preference

Table 1. The LANDIS-II Browse Extension user-defined parameter estimates used in model applications at the ANF and ISRO.

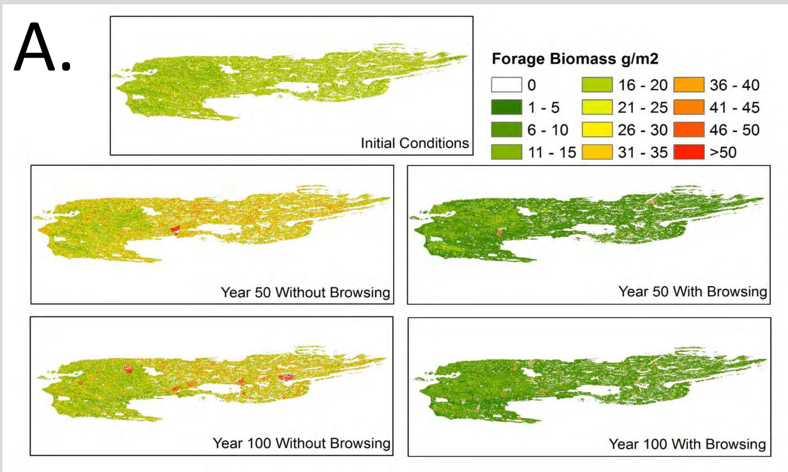
A.		Growth Reduction		Mortality	
Species	Preference	Threshold	Max	Threshold	Max
F. grandifolia[1,3,5]	0.330	0.20	0.55	0.95	0.05
A. rubrum[1,3,5]	0.600	0.10	0.70	0.75	0.15
A. saccharum[1,3,5]	0.495	0.10	0.80	0.75	0.15
B. alleghaniensis[1,3,4,5]	0.400	0.15	0.70	0.90	0.15
B. lenta[1,3,5]	0.400	0.15	0.70	0.90	0.15
P. serotina[1,3,5]	0.165	0.15	0.40	0.90	0.20
General Quercus[1,4,5]	0.600	0.10	0.40	0.80	0.15
Q. rubra[1,5]	0.600	0.10	0.40	0.80	0.15
T. canadensis[1,2,5]	0.495	0.20	0.80	0.75	0.50

B.		Growth Reduction		Mortality	
Species	Preference	Threshold	Max	Threshold	Max
A. balsamea[1,2,4,6]	0.15	0.2	0.6	0.8	0.1
A. saccharum[2,3,6]	0.15	0.2	0.6	0.8	0.1
B. alleghaniensis[2,3,6]	0.15	0.2	0.6	0.8	0.1
B. papyrifera[2,5,6]	0.25	0.5	0.4	0.9	0.1
F. nigra[1,2,6]	0	0	1	0.8	0.1
Other Deciduous[1,2,6]	0.25	0.5	0.4	0.9	0.1
P. banksiana[1,2,6]	0	0	1	0.8	0.1
P. glauca[1,2,6]	0	0	1	0.8	0.1
P. mariana[1,2,6]	0	0	1	0.8	0.1
P. tremuloides[1,2,3,6]	0.30	0.5	0.4	0.9	0.1
T. occidentalis[1,2,6,7]	0.05	0.2	0.6	0.8	0.1

Tables 2 A and B: Browse disturbance parameters for the ANF(A), and ISRO(B). Preference values are used to rank species according to herbivore browse preference and define a target proportion of available forage biomass removed at a site during a given time step. Growth reduction and mortality parameters define a threshold proportion of available forage biomass removed that triggers a growth or mortality response, and a maximum growth or mortality response when 100% of available forage biomass is removed.

Results and Discussion

Across both study areas, observational and experimental work has consistently demonstrated that moderate to high browsing delays, alters, and even prevents forest regeneration. Browsing caused a strong reduction in total aboveground biomass (Figs. 4 & 5) despite the fact that the population was removing a small fraction of annual net primary productivity. Our results suggest that not accounting for browsing by dense ungulate populations may result in an over prediction of aboveground biomass and the abundance of species that are highly preferred and/or not tolerant of tissue removal.



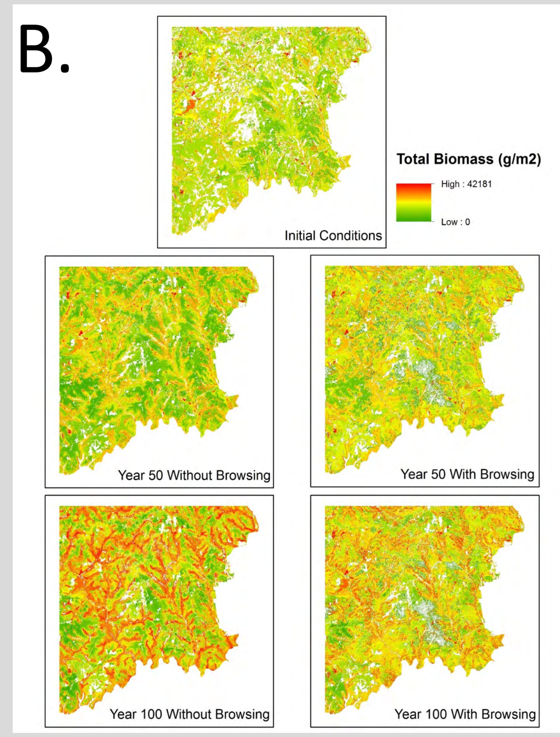


Fig. 4. Changes to the distribution of available forage biomass at ISRO(A) and ANF(B) over a 100 year period with and without simulated deer browsing. Browsing causes an overall reduction in total biomass across the landscape.

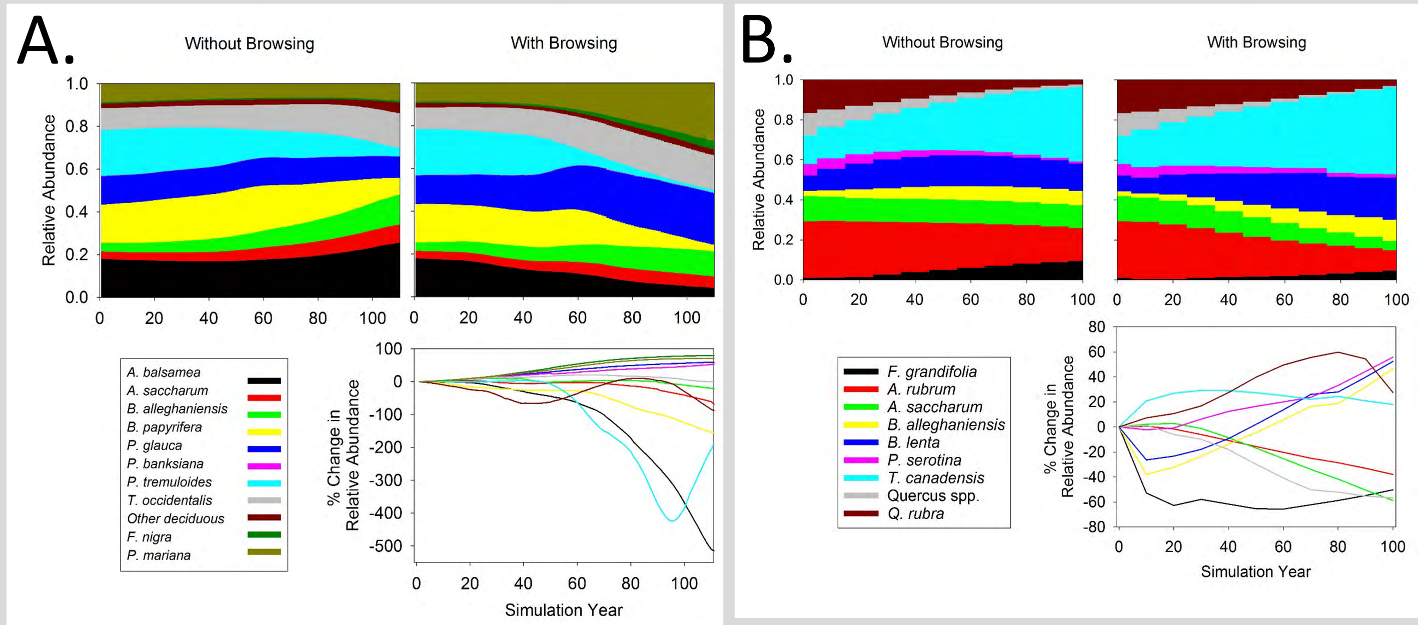


Fig. 5. The composition of total above ground live biomass for model simulations with and without browsing at ISRO (A) and ANF(B). Note that browsing causes a shift in composition away from the most highly preferred species and toward less preferred species.

Implications for Soil Science

While the biomass succession extension that we employed here does track and model litter and wood decay, it does not extend these calculations to soil fertility. Future modelling efforts could extend browsing impacts to soil fertility by integrating the browse extension with the LANDIS II Century succession extension (Scheller et al. 2011), which models below ground processing of carbon and nitrogen following the logic of the Century nutrient cycling model (v4.0).